

## SECONDARY DISPERSAL OF WILLOW SEEDS: SAILING ON WATER INTO SAFE SITES

JOHN M. BOLAND

Boland Ecological Services, 3504 Louisiana Street, San Diego, CA 92104  
JohnBoland@sbcglobal.net

### ABSTRACT

Willows (*Salix* spp.) produce many small seeds that are dispersed primarily through the air by winds (anemochory) and sometimes secondarily by flowing water (hydrochory). In this paper I identify another way willow seeds are dispersed – being blown by winds while sailing or floating on the surface of standing water, here termed pleustochory. In experiments, seeds of *Salix gooddingii* C.R. Ball floated on water for four days and sailed swiftly on the surface of pools when light winds blew, reaching speeds in excess of five meters per minute. Field observations showed that *S. gooddingii* seeds sailing on water were blown downwind and soon came to rest at the edge of the pool, in their preferred safe sites. This dispersal via pleustochory from unsuitable sites (middle of a pool) into safe sites (edge of pool) is therefore a new example of directed dispersal. *Salix gooddingii* seed dispersal and seedling densities were studied at a large, remote pool in the Tijuana River Valley, San Diego Co., to examine the influence of pleustochory on *S. gooddingii* seedling densities. The study focused on a 15-day period when the pool was slowly drying and *S. gooddingii* seeds were dispersing from a distant, isolated stand. The *S. gooddingii* seedlings that established during the 15-day period formed a band that encircled the entire pool with the highest densities (3140 seedlings per m<sup>2</sup>) occurring along the On Shore. The numbers of *S. gooddingii* seeds arriving in the seedling sites via three dispersal routes – hydrochory, anemochory, and pleustochory – were measured or estimated. A model combining all three dispersal routes accurately predicted the pattern of seedling densities around the pool and estimated that pleustochory accounted for more than 99% of the seedlings along the On Shore. Together these results showed that pleustochory played a vital role in the transport of *S. gooddingii* seeds to safe sites and was the underlying mechanism producing the pattern of seedling densities around a large pool.

Key Words: Anemochory, directed dispersal, hydrochory, pleustochory, *Salix gooddingii*, secondary dispersal, seed dispersal, willows.

### INTRODUCTION

Wind is a common dispersal agent of seeds. Wind dispersal can occur in two phases: an initial, often long-distance, airborne movement of seeds from the mother plant to the ground, called primary dispersal; and a usually shorter, wind-driven movement along the ground, called secondary dispersal (Watkinson 1978; Chambers and MacMahon 1994; Greene and Johnson 1997). Secondary dispersal can greatly affect the microhabitat a seed finally settles in and the overall seed shadow (Nathan and Muller-Landau 2000). This is particularly true if the seeds are mobile, if the ground surface is smooth, if there are few obstacles to impede seed movement, and if there are high velocity winds close to the ground (Bond 1988; Johnson and Fryer 1992; Greene and Johnson 1997). Secondary dispersal is considered more likely to account for the patterning of plants in communities, but it has been poorly studied and has been considered “our greatest knowledge gap” (Chambers and MacMahon 1994, p. 266).

Willows (*Salix* spp.) are pioneer tree species that dominate young riparian forests in southern California (Faber et al. 1989; Boland 2014).

Willows produce large numbers of tiny, short-lived seeds that are dispersed at first by wind through the air and sometimes secondarily by flowing water (Karrenberg et al. 2002) or by wind along the ground (Seiwa et al. 2008). Each seed is enveloped by a ring of long, cottony hairs that provide buoyancy both in air and on water (Steyn et al. 2004; Seiwa et al. 2008). The aerial seed rain for wind-dispersed species, such as willows, is typically leptokurtic with seed density peaking near the parent plant and rapidly declining with distance outwards (Willson 1983), often resulting in surprisingly low seed densities in the seed rain only a few hundred meters from parent plants (Gage and Cooper 2005). Willows take advantage of disturbances caused by winter and spring flood flows, and seed production, seed dispersal, and seedling establishment occur soon after the highest flows (Stella et al. 2006; Boland 2014). Safe sites (Harper 1977) for the germination of willow seeds are disturbed, vegetation-free, moist substrates that typically occur in a narrow band at the water’s edge of pools and streams (Mahoney and Rood 1998; Seiwa et al. 2008). These moist substrates are sometimes called the “capillary fringe” (Mahoney and Rood 1998, p. 640). How willow seeds arrive in these safe sites

is not well understood, however, because secondary dispersal in willows has received little attention.

Pools are common along the stream and river courses in coastal southern California during spring and early summer when willow seeds are dispersing. Most of these waterways have intermittent flows and are reduced to widely-spaced pools soon after the last heavy rains of the season (Faber et al. 1989; Boland 2014). Using a variety of approaches, I investigated the secondary dispersal of willow seeds on pools. I tested the general hypotheses that there is secondary dispersal of seeds on pools and that it influences the patterning of plants in communities. In particular, I: (1) examined the floating ability of willow seeds on water; (2) measured the speed at which willow seeds sailed on water; and (3) compared the influence of different seed supply routes on willow seedling densities around a remote pool, comparing seed supply from the air (anemochory), via flowing water (hydrochory), and via the surface of standing water (which I call pleustochory). This study is one of very few that simultaneously quantifies primary dispersal, secondary dispersal, and post-dispersal seedling densities.

## METHODS

### Study Species and Study Site

This research was conducted on *Salix gooddingii* C.R. Ball (Goodding's black willow, Salicaceae) within the Tijuana River Valley (32°33.080'N, 117°4.971'W) in San Diego County, California. The Tijuana River is an intermittent stream that flows strongly during winter and spring, and then becomes a series of a few widely-spaced pools in summer (Zedler et al. 1992). *Salix gooddingii* is one of the most abundant species in the riparian habitats of the valley (Boland 2014) and was the only common willow fruiting during the course of this study (late May to July 2013). Like many other willows, seeds are small (~1 mm long) and each is surrounded by a plume or coma of hollow, cottony hairs (~10 mm long) that is attached to the seed by a ring structure, the hilar aril. These hairs develop from either the placenta (Takeda 1936) or the funicle (Steyn et al. 2004) and serve as a parachute for the seed.

### Seed Behavior

**Floating ability.** The floating ability of *S. gooddingii* seeds was examined in the laboratory. A total of 60 seeds, with their cottony hairs, were placed on water (1.5 cm deep) in five shallow dishes (9-cm diameter; 12 seeds per dish) and floating monitored for four days. For the purposes of this study, the ability of the seeds

to float for a few minutes or hours after landing on water was more important than the total length of time they floated. Seeds were therefore monitored frequently at first (every 30 min during the first three hours and every hour during the next seven hours) and less frequently thereafter (every three to ten hours for the remaining four days). The floating period was defined as the length of time between the placement of a seed on the water surface and the seed sinking (Seiwa et al. 2008).

**Sailing speed.** The speed at which *S. gooddingii* seeds sailed on the water was measured at a typical small pool in the Tijuana River during June 2013. The pool was near the Dairy Mart Road bridge and was 20 m × 4.4 m in size and less than one m deep. A single *S. gooddingii* seed, with its coma of cottony hairs, was dropped onto the water surface, and the distance it sailed during 30 seconds was measured. Simultaneously, the average wind speed during the 30 second period was measured nearby (within 10 m) by an assistant holding a Kestrel 3000 Pocket Weather Meter (Nielsen-Kellerman Company, Bothwyn, PA) one m above the water's surface and into the wind. These winds were in the Beaufort categories of "calm" to "light breeze" (<204 m per minute). Twenty seeds were run on each day for three days (n = 60 seeds).

### Seed Dispersal and Seedling Densities

**Goat Canyon pool.** Primary seed dispersal, secondary seed dispersal, and post-dispersal seedling densities were studied at a large (275 × 45 m), unvegetated pool in the western Goat Canyon sedimentation basin in the Tijuana River Valley (Fig. 1). The pool was crossed in the west by a trash boom that consisted of three m-long plastic floats with a 0.5 m gap between each float (Tuffboom by Worthington Products, Inc., Canton, OH). No trash was caught on the boom at the time of the study, and willow seeds and other small floating objects were slowed but not stopped by the boom. The study focused on a 15-day period (19 May to 3 June 2013) when *S. gooddingii* plants were dispersing seeds (Boland 2014) and the pool was slowly drying. During this period the water level dropped 14 cm and the pool surface area decreased from 10,142 to 9008 m<sup>2</sup>. Initial and final pool water levels and boundaries were measured with a Trimble R8 Model 2 GNSS rover GPS unit (Trimble Navigation Ltd., Sunnyvale, CA).

The Goat Canyon pool was an ideal place to study *S. gooddingii* dispersal and seedling densities for several reasons. First, there was no surface inflow during the study period so there was no introduction of seeds via flowing water, i.e., hydrochory was not a factor. The last inflow

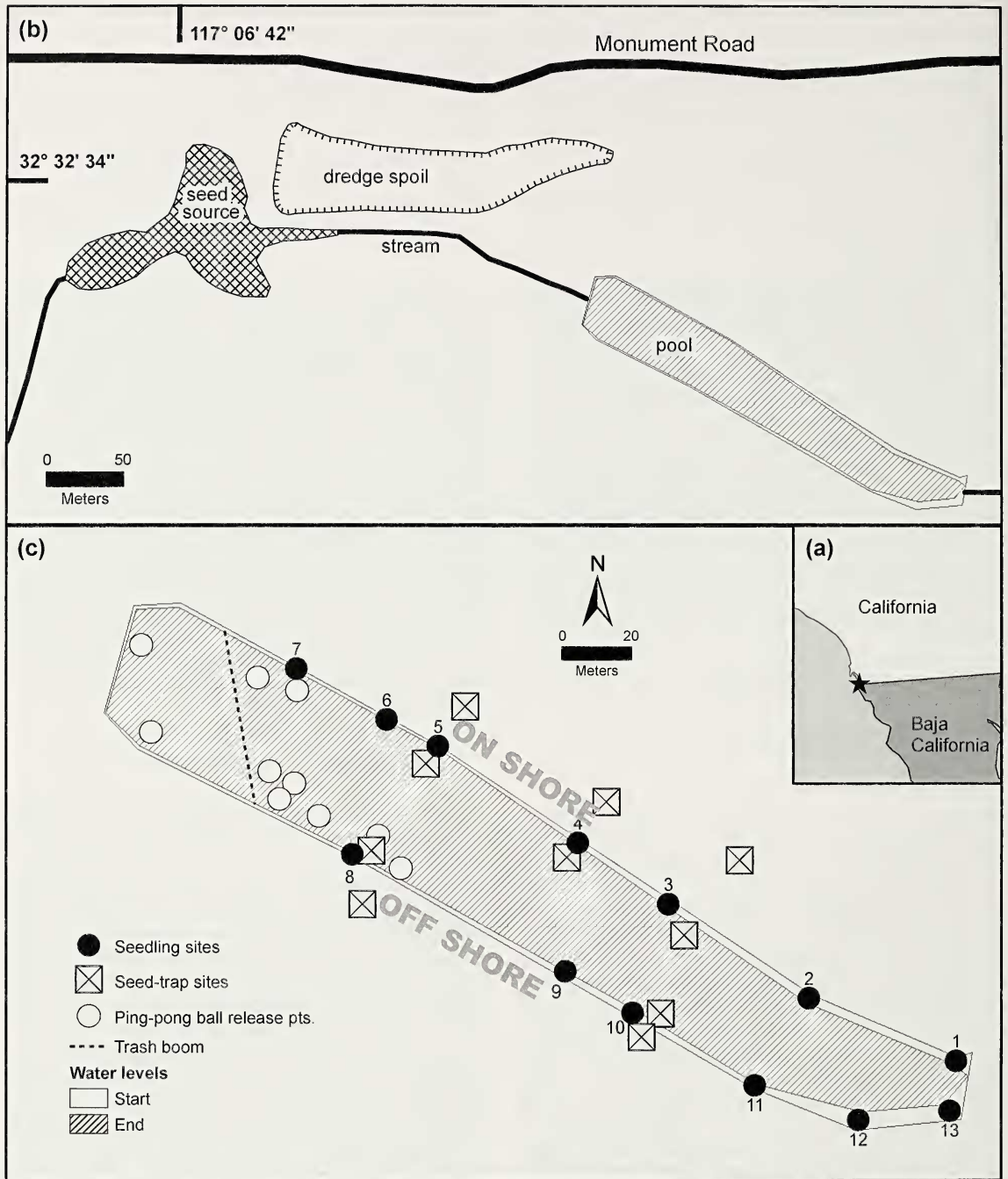


FIG. 1. Maps of the study area. (a) Overview of the California coast showing the location of the Tijuana River Valley. (b) View of the Goat Canyon sedimentation basin area showing the location of the pool and the *S. gooddingii* seed source. (c) Close up view of the Goat Canyon pool showing the seedling sites, seed-trap sites and ping-pong ball release points. It also shows the water levels at the start and end of the 15-day study period.

occurred on 6 May 2013, 13 days before the start of the study period, and the next inflow occurred well after the seedlings had been counted. Second, the main source of *S. gooddingii* seeds was an isolated, dense stand to the west, which meant that seeds arrived at the pool from only one direction and only when westerly winds blew

(Fig. 1). The pool's two main shores were named according to their position relative to westerly winds, i.e., the Off Shore (west) and the On Shore (east) (Fig. 1c). The wind rose for the 15-day study period shows that westerly winds blew for approximately 12% of the time (Fig. 2). Third, there were no windbreaks near the pool to

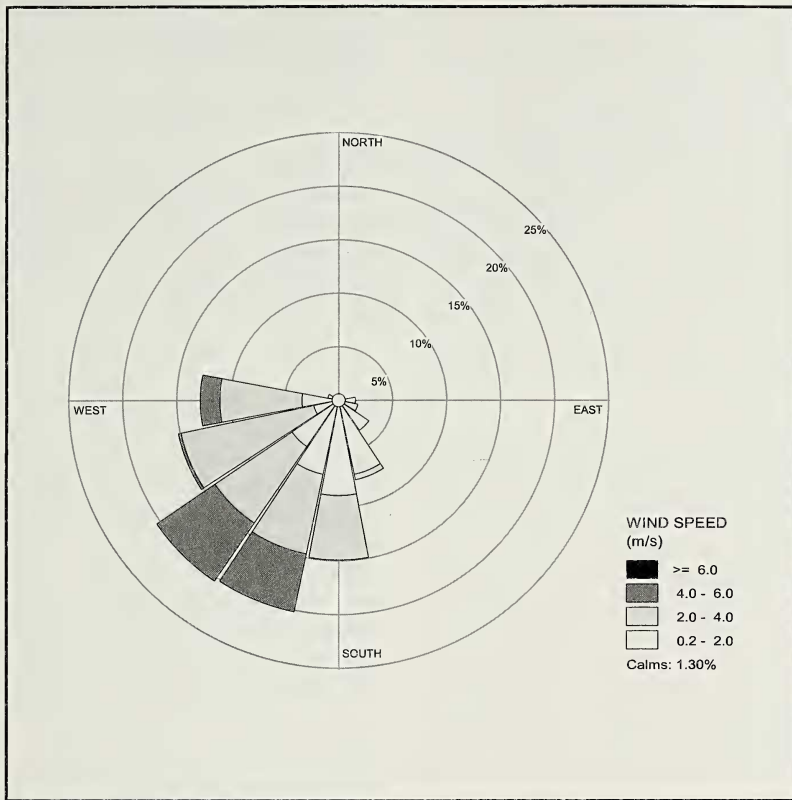


FIG. 2. The wind rose for the 15-day study period. The data are from a weather station 4 km due north of the Goat Canyon pool.

prevent winds from reaching the surface of the pool; the closest perennial vegetation consisted of low-growing shrubs more than 10 m from the water's edge. Fourth, the entire shoreline around the pool was suitable for the recruitment of *S. gooddingii* seedlings. Bulldozers had emptied the basin during September 2012 and rains had refilled it with suitable sediment during winter 2012–2013.

*Seedling densities.* The seedlings of interest were those that established during the 15-day study period (19 May to 3 June 2013) at the Goat Canyon pool. The water levels at the start and end of the period were marked with many stakes around the pool's edge, and *S. gooddingii* seedlings that recruited into the newly exposed zone between those levels were counted soon after they grew their first few leaves and could be identified to species (July 2013). The counts were conducted at 13 sites that were located in a stratified random manner (Fig. 1). At each site, two transects were placed parallel to the water's edge in a stratified random manner in the upper and lower halves of the zone. Along each transect, seedlings were counted within ten quadrats ( $20 \times 20$  cm) placed at one m intervals (i.e., 20 quadrats per site). A total of 10,605 *S.*

*gooddingii* seedlings were counted in the 260 quadrats. Seedlings densities of the Off Shore and On Shore sites were tested for significant differences using the Mann-Whitney U-Test (Sokal and Rohlf 1995).

In addition, sediment grain size, a potentially important physical characteristic, was measured by taking a sediment core (7.2 cm diameter  $\times$  5 cm deep) at the five m point along the lower transect at each site. Approximately 100 g of dried sediment from each core was shaken through two sieves (U.S. Standard Mesh #35 and #230) that separated the sediment into three size classes: coarse sand, fine sand, and silt. Each size-class fraction was weighed and expressed as a percentage of the total at each site. Sediment grain sizes from the Off Shore and On Shore were tested for significant differences using the Mann-Whitney U-Test (Sokal and Rohlf 1995).

*Primary dispersal – aerial seed rain.* The density of *S. gooddingii* seeds in the aerial seed rain was estimated by deploying 120 seed traps over the water and around the Goat Canyon pool. Five seed-trap sites were chosen in a stratified random manner. At each site, 12 traps were placed over the shallow water and 12 traps were placed on the bank (Fig. 1). Each group of 12 traps was

arranged in an array of  $3 \times 4$  where each was one m from its neighbor. The traps were constructed of 500 ml plastic water bottles with their bottoms cut off. They were attached upside down to wooden stakes, thereby exposing an opening of 6.6 cm in diameter on the top for seeds to fall into. The traps were in the field for the 15-day study period (19 May to 3 June) and then bagged and collected. The contents were examined under a dissecting microscope and the number of *S. gooddingii* seeds counted. The strength of the link between the number of seeds per trap and the trap's distance from the seed source was quantified using correlation analysis (Sokal and Rohlf 1995).

*Secondary dispersal – seeds and seed mimics on the water.* The dispersal of *S. gooddingii* seeds on the water surface was observed from many points around the Goat Canyon pool under varied wind and water conditions. Of particular interest were the directions in which the floating seeds sailed and the behavior of floating seeds when they reached the edge of the pool. Because it was difficult to follow individual seeds as they sailed across the pool (>40 m), ping-pong balls were used to simulate the sailing of seeds on the water. Ping-pong balls (Family Maid by Dollar Empire LLC, Vernon, CA; recreational grade; 40 mm diameter; 2.7 g) were good mimics for *S. gooddingii* seeds because they sailed at the same speed and, most importantly, in the same direction as the seeds. A preliminary test on the Goat Canyon pool showed no significant difference in the direction of dispersal of ping-pong balls and *S. gooddingii* seeds (Mann-Whitney  $U = 284$ ,  $n_1 = n_2 = 24$ ,  $P > 0.05$ ).

To simulate the secondary dispersal of *S. gooddingii* seeds on the pool, groups of 24 balls were released from 10 locations on the pool (Fig. 1) when westerly winds were blowing, and their dispersal tracks and destinations were mapped. All 240 balls (100%) were retrieved. The tracks of the actual balls were then converted to tracks of virtual balls originating from evenly-spaced points covering the entire pool. A grid of evenly-spaced (five m apart) virtual balls ( $n = 436$ ) was placed over the map of the actual ball tracks and each virtual ball followed the track of the nearest actual ball to its destination at the pool's edge. The number of virtual balls landing in each seedling site (with 10 m shoreline length) was counted.

*Seedling densities – predicted vs. actual.* To test the hypothesis that secondary dispersal of seeds influences the patterning of plants in communities, a simple model was developed to predict the density of seedlings found in each of the seedling sites around the Goat Canyon pool. The predicted number of seedlings per  $m^2$  in a site ( $SL_{PREDICTED}$ ) is the sum of the seedlings that

grew from seeds that arrived via hydrochory ( $SL_H$ ), anemochory ( $SL_A$ ), and pleustochory ( $SL_P$ ), i.e.,

$$SL_{PREDICTED} = SL_H + SL_A + SL_P$$

In this study, the number of seedlings growing from seeds that arrived via hydrochory ( $SL_H$ ) was zero because the pool received no inflow during the study period. The number of seedlings growing from seeds that arrived via anemochory ( $SL_A$ ) was estimated to be:

$$SL_A = S_A \cdot W_{CF} \cdot L_{CF} / W_{SS} \cdot L_{SS}$$

where  $S_A$  is the average number of seeds caught in the seed traps during the study period (expressed as seeds per  $m^2$ );  $W_{CF}$  and  $W_{SS}$  are the average width of the capillary fringe (i.e., safe site) and the total width of the seedling site during the study period, respectively, as measured perpendicular to the water's edge (m); and  $L_{CF}$  and  $L_{SS}$  are the lengths of the capillary fringe and the seedling site, respectively, as measured parallel to the water's edge (m). In these calculations  $L_{CF}$  and  $L_{SS}$  were set at one m and  $SL_A$  was expressed as number of seedlings per  $m^2$ . The ratio  $W_{CF} \cdot L_{CF} / W_{SS} \cdot L_{SS}$  is required because only a narrow capillary fringe is suitable for seedling recruitment and it moved slowly through the seedling site as the water level declined.

The number of seedlings growing from seeds that arrived via pleustochory ( $SL_P$ ) was estimated as:

$$SL_P = S_A \cdot F / W_{SS} \cdot L_{SS}$$

where  $F$  is the 'fetch' ( $m^2$ ), i.e., the strip of the pool's surface (one m wide) that was on the path from the source *S. gooddingii* plants to the seedling site, and  $S_A$ ,  $W_{SS}$  and  $L_{SS}$  are as above. In these calculations  $L_{SS}$  was set at one m and  $SL_P$  was expressed as number of seedlings per  $m^2$ . This equation formalizes the idea that all of the seeds that landed on the fetch during the study period sailed downwind to the seedling site where they germinated and became established.

Notice that both  $SL_A$  and  $SL_P$  are based on only physical characteristics of the site and the number of seeds caught in the seed traps. The model's predicted densities of seedlings in the seedling sites were compared to the actual seedling densities using correlation analysis (Sokal and Rohlf 1995).

## RESULTS

### Seed Behavior

*Floating ability.* All 60 *S. gooddingii* seeds floated on the water's surface and remained

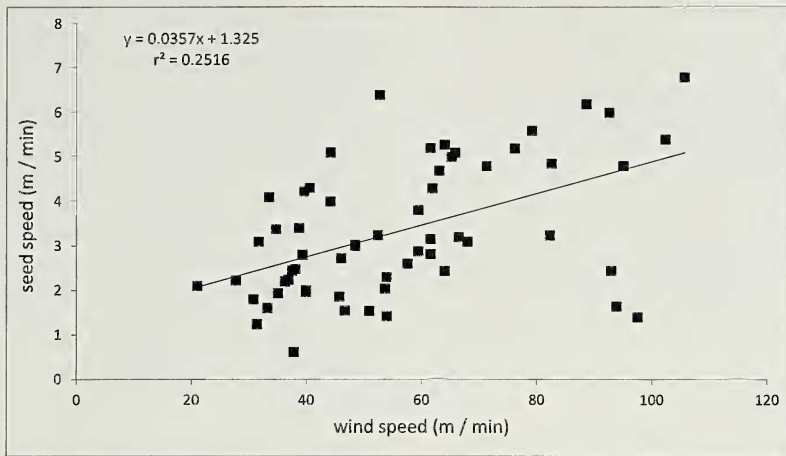


FIG. 3. The speed of *S. gooddingii* seeds sailing on the water surface. The equation and coefficient of determination are shown for the linear regression line.

floating for the full four days. The cottony hairs did not become water-logged, and the seeds were not released from their enveloping coma of hairs. *Salix gooddingii* seeds therefore float when first landing on water and have the ability to stay afloat for days.

**Sailing speed.** *Salix gooddingii* seeds were blown downwind while floating on the surface of the water. They sailed swiftly over the surface of the pool even when only light breezes were blowing. The seeds sailed quicker when the breeze was stronger and reached speeds in excess of 5 m per minute during the experiment (Fig. 3;  $r^2 = 0.251$ ,  $n = 60$ ,  $P < 0.06$ ). It took only a few minutes for a seed to sail the length of the small pool (20 m).

#### Seed Dispersal and Seedling Densities

**Seedling densities.** *Salix gooddingii* was the most abundant species within the seedling community that developed in the zone exposed during the 15-day study period at the Goat Canyon pool. Its seedlings formed a band that encircled the entire pool with average densities from 68.8 to 3140 seedlings per  $m^2$  (Sites 10 and 5, respectively; Table 1). Seedling densities were lowest along the Off Shore (particularly in Sites 9–12) and highest along the On Shore (particularly in Sites 3–5), and there was a significant difference in densities on the two shores (Mann-Whitney  $U = 7.4$ ;  $n_1 = 7$ ;  $n_2 = 6$ ;  $P < 0.01$ ).

Sediment grain sizes were similar at all sites, with fine sands and silts dominating (Table 1). There was no significant difference in the composition of the sediments on the Off Shore and On Shore (Mann-Whitney  $U = 23$ ;  $n_1 = 7$ ;  $n_2 = 6$ ;  $P > 0.05$ ).

**Primary dispersal – aerial seed rain.** A total of 28 *S. gooddingii* seeds were caught in the seed

traps at the Goat Canyon pool during the 15-day period, for an average of  $68.2 (\pm 14.6 \text{ std. err.}; n = 120)$  seeds per  $m^2$ . There was no correlation between the number of seeds in a trap and the distance of the trap from the seed source ( $r^2 = 0.1015$ ;  $n = 10$ ;  $P > 0.05$ ) suggesting that, at this distance from the source ( $>250$  m), the seed rain over the pool was sparse and approximately evenly distributed.

**Secondary dispersal – seeds and seed mimics on the water.** *Salix gooddingii* seeds were blown from their source trees to the Goat Canyon pool when westerly winds blew (Fig. 1). Seeds that landed on the pool continued to be blown by the westerly wind across the surface of the pool to the water's edge along the On Shore. At the water's edge seeds often accumulated with other floating plant debris, such as flocculent algae, pollen and leaves. Each day this mix of floating debris was deposited along the On Shore by the largest breaking waves and highest wind surges of the day. When the seeds were washed against the firm shoreline sediment they were separated from their cottony hairs and their dispersal was ended. Because the water level in the Goat Canyon pool was declining at a rate of  $\sim$ one cm per day and exposing  $\sim$ 10 cm of shore per day, the stranded debris was left in distinctive lines, known as windrows or wrack lines,  $\sim$ 10 cm apart. These windrows extended for tens of meters along the shoreline. Later, the seedlings were distributed in the same distinctive windrows.

The ping-pong balls provided a clear view of where seeds sailed on the pool's surface. All 240 balls (100%) were blown by westerly winds across the pool to the On Shore. Even balls released near the Off Shore ended up on the On Shore. These observations confirmed that sites around the pool were receiving seeds from the pool's surface and, due to the location of the source trees and

TABLE 1. CHARACTERISTICS OF THE 13 SEEDLING SITES AROUND THE GOAT CANYON POOL. The physical characteristics of the sites, the densities of virtual balls arriving in the sites via pleustochory, and the actual and predicted number of *S. gooddingii* seedlings in each site; cs = coarse sand; fs = fine sand; s = silt; and fetch area = overwater length × one m width.

Site	Shore	Width of site (W <sub>ss</sub> ) (m)	Sediment composition (%cs:%fs:%s)	Distance from seed source (m)	Fetch area (F) (m <sup>2</sup> )	Virtual balls (#/10 m of shore)	Actual # seedlings		Predicted # seedlings					Total (SL <sub>PREDICTED</sub> ) (#/m <sup>2</sup> )
							mean (#/m <sup>2</sup> )	std error (#/m <sup>2</sup> )	Hydrochory (SL <sub>H</sub> ) (#/m <sup>2</sup> )	Anemochory (SL <sub>A</sub> ) (#/m <sup>2</sup> )	Pleustochory (SL <sub>P</sub> ) (#/m <sup>2</sup> )			
1	On	2.2	8 : 44 : 28	558	137	18	877.5	79.8	0	13	4238	4251		
2	On	2.8	6 : 66 : 28	512	113	15	1076.3	205.2	0	10	2760	2770		
3	On	2.2	2 : 64 : 34	466	116	18	1981.3	206.3	0	13	3608	3621		
4	On	1.1	3 : 73 : 24	447	118	28	2065.0	177.0	0	13	7331	7344		
5	On	0.9	7 : 79 : 14	402	102	25	3140.0	415.0	0	16	7923	7939		
6	On	1.0	14 : 77 : 9	388	88	19	1666.3	96.7	0	14	6129	6143		
7	On	1.3	12 : 73 : 15	350	45	11	598.8	71.2	0	10	2359	2369		
8	Off	1.0	15 : 70 : 15	374	0	1	413.8	72.2	0	14	0	14		
9	Off	1.4	6 : 79 : 15	441	0	1	107.5	16.8	0	10	0	10		
10	Off	2.4	9 : 77 : 14	463	0	1	68.8	24.5	0	11	0	11		
11	Off	1.6	5 : 64 : 31	513	0	1	130	49.9	0	17	0	17		
12	Off	5.4	11 : 53 : 36	536	0	4	147.5	49.6	0	8	0	8		
13	Off	6.7	31 : 62 : 7	561	83	25	983.8	172.5	0	6	840	846		

necessary wind direction, On Shore sites were receiving the majority of the seeds that landed on the pool.

When the tracks of the actual ping-pong balls were converted into tracks of evenly-spaced virtual balls, nearly all of the virtual balls ended up on the On Shore (Table 1). Because each virtual ball represented a particular area of the pool's surface, an accumulation of many virtual balls in a site meant that the site had received balls from a large area of the pool's surface. This area of the pool is the fetch for that seedling site. The configuration of the pool in relation to the source plants meant that some seedling sites had a large fetch whereas others had none at all (Table 1).

*Salix gooddingii* seeds that landed in the dry areas around the Goat Canyon pool were observed to become stuck, either on plants or on rough ground. There was no indication that seeds that landed in these dry areas were later blown to safe sites at the water's edge.

*Seedling densities - predicted vs. actual.* The mathematical model accurately predicted the pattern of seedling densities around the Goat Canyon pool (Table 1). The model predicted that seedling densities would be highest along the On Shore (particularly in Sites 4-6) and lowest along the Off Shore (particularly in Sites 8-12). The predicted and actual number of seedlings at the sites were significantly correlated ( $r^2 = 0.827$ ;  $n = 13$ ;  $P < 0.01$ ). An important component of the model was the size of the fetch, and the fetch for each site was positively and significantly correlated with the number of seedlings in a seedling site ( $r^2 = 0.570$ ;  $n = 13$ ;  $P < 0.01$ ). Where there was a long fetch between the source and the seedling site the site had many seedlings, whereas if there was little or no fetch between the source and the seedling site the site had few seedlings (Table 1).

DISCUSSION

Sailing on the Water Surface - Pleustochory

When *S. gooddingii* seeds land on a pool, they float on the water's surface and sail quickly with the breeze across the surface. As there is currently no term for the dispersal of seeds by wind while floating on standing water, I have coined the term **pleustochory** from the Greek words "pleust" "to sail" or "to float" and "chore" "to move." This form of dispersal (pleustochory) is differentiated from anemochory, in which seeds are dispersed by wind and carried in air, and from hydrochory, in which seeds are carried downstream by flowing water (van der Pijl 1982). The prefix "pleust" already appears in the scientific literature as pleuston, the name given to the group of plants (e.g., *Lemma* spp., *Azolla* spp., *Sargassum* spp.)

and animals (e.g., *Veleva veleva*) that are free-floating at the air-water interface of a body of water and are dispersed by winds while floating on water (Wetzel 1983). The term pleustochory should also include the dispersal of seeds and seedlings that float at the water's surface and are transported by wind-driven water movements (Soomers et al. 2010; Sarneel et al. 2014).

Wind-driven seed dispersal along the ground has been studied in many species and situations. It has been documented in temperate grasslands (van Tooren 1988), coastal environments (Watkinson 1978), alpine habitats (Chambers et al. 1991), arid and semiarid environments (Aguar and Sala 1997), on snow (Matlack 1989; Greene and Johnson 1997), as well as in environments disturbed by fire (Bond 1988), human activities (Campbell et al. 2003) and volcanic eruptions (Fuller and del Moral 2003). In general, these studies have found that dispersal by wind over the ground occurs only under certain conditions: when seeds remain mobile for sufficient periods of time; when the ground surface is smooth; when few obstacles impede seed movement; and when winds reach the ground. Such conditions are rarely met for seeds on the ground and, in general, wind-blown seeds usually move only short distances on the ground before becoming trapped on plants or in crevices (Chambers and MacMahon 1994). These conditions are easily met for willow seeds on water, however. The seeds remain mobile for days, the water surface is smooth, there are few obstacles, and winds reach the surface of the water. The result is that willow seeds can quickly travel tens of meters or more on the water's surface.

The seeds of *S. gooddingii* can float and sail because they are small, light, and surrounded by a coma of long, hollow hairs (Steyn et al. 2004; Seiwa et al. 2008). Many other riparian and wetland species have small, cottony seeds similar to *S. gooddingii* and are also likely to be able to sail; these species include other willows (*Salix* spp.), cottonwoods (*Populus* spp.), cattails (*Typha* spp.), tamarisk (*Tamarix* spp.), and many Asteraceae (e.g., *Baccharis* spp.). Pleustochory therefore may be a common mode of dispersal in many riparian and wetland plant species.

#### Sailing into Safe Sites – Directed Dispersal

The secondary dispersal of *S. gooddingii* seeds by pleustochory results in seeds traveling from the middle of a pool to the edge of a pool. For *S. gooddingii* and other willows, safe sites are vegetation-free, moist substrates that typically occur at the water's edge around disturbed pools and along stream banks (Mahoney and Rood 1998; Seiwa et al. 2008). In these safe sites, willow seeds germinate successfully and seedling establishment is high (Boland 2014). The secondary

dispersal of *S. gooddingii* seeds by pleustochory therefore results in seed movement from unsuitable sites (middle of a pool) to safe sites (edge of a pool), and is an example of directed dispersal, i.e., the non-random dispersal to sites especially favorable for successful germination and seedling establishment (Howe and Smallwood 1982; Wenny 2001; Seiwa et al. 2008).

Most examples of directed dispersal involve the action of an animal vector, i.e., an ant, bird, or mouse carries the seed away from the parent plant or ground surface to a more suitable germination site (e.g., Herrera and Jordano 1981; Wenny and Levey 1998). Some researchers have even questioned whether it is possible for winds to move seeds in a non-random manner with respect to establishment sites (e.g., Vander Wall and Longland 2004). But winds can concentrate seeds into safe sites if the safe sites are structurally different to their surroundings; in this study, *S. gooddingii* seeds were easily blown across the smooth surface of the Goat Canyon pool but became stuck in the rough, muddy edge, which is their safe site. In addition, Seiwa et al. (2008) found under experimental conditions that willow seeds can be blown over dry sand and trapped in wet sand and therefore blown from less suitable to more suitable microsites, although dispersal of this type has not been documented under natural conditions. Also, winds can concentrate seeds into safe sites when wind speed or direction is changed by an obstacle or vegetation gap. Winds in and around forest gaps were found to carry seeds of shade-intolerant plants from surrounding forested areas into sunny forest gaps, more suitable for their germination and growth (Augspurger and Franson 1988). So, contrary to the prevailing view of Vander Wall and Longland (2004) and others, winds can disperse seeds non-randomly and can play a role in their directed dispersal into establishment sites.

Directed dispersal is difficult to identify in most systems and may be more common and ecologically significant than previously believed (Wenny 2001). Directed dispersal is difficult to identify because: (1) following a dispersing seed from its parent to its final destination is difficult; (2) safe sites are often difficult to specify or are poorly known for most species; and (3) determining which seeds from a cohort germinate successfully can be complicated by dormancy and the presence of other cohorts in the seed bank (Wenny 2001). Willows, however, have characteristics that make directed dispersal comparatively easy to detect: easily-followed seed production (Stella et al. 2006; Boland 2014); relatively easily-followed primary and secondary dispersal (Gage and Cooper 2005, this study); well-known and easily identified safe sites (Seiwa et al. 2008); and immediate germination with no seed dormancy or seed bank (Emery 1988; Stella et al.



2006; Karrenberg et al. 2002). The willows of southern Californian riparian ecosystems are therefore excellent species in which to test dispersal hypotheses.

### Pleustochory and Seedling Densities

The general hypothesis that the secondary dispersal of seeds on pools influences the patterning of plants was confirmed. First, direct observations showed that, when westerly winds were blowing, most of the seeds (and ping-pong balls) that landed on the Goat Canyon pool were blown across the water to the On Shore. Second, seedling densities along the On Shore were very dense – up to 3140 seedlings per m<sup>2</sup> or more than 45 times the density of seeds arriving in the aerial seed rain, the only other mode of seed transport into these sites at that time. Third, a model derived from only the number of seeds in the aerial seed rain and physical characteristics of the sites correctly predicted the pattern of seedling densities around the Goat Canyon pool and estimated that 99% of the seedlings on the On Shore came from pleustochory. Finally, the seedlings on the On Shore were growing in distinctive windrows, a sure sign that the seeds had arrived from the water rather than from the air (Glaser 1981). Together, these lines of evidence indicated that secondary dispersal via pleustochory produced the striking seedling density pattern around the Goat Canyon pool.

Many authors point to the high mortality rates of willow seedlings during their first summer as an important limiting feature of young riparian communities (e.g., Karrenberg et al. 2002). But the effect of high mortality can be greatly offset by initially high seedling densities; even if 90% of seedlings die in their first summer, enough will survive their first year to form a thriving thicket the following year. In an earlier study in the Tijuana River Valley (Boland 2014), *S. gooddingii* seedlings had a 92% mortality rate during their first year but formed dense thickets by the start of their second year (~20 yearlings per m<sup>2</sup> and ~1.7 m tall), and went on to form tall, dense stands three years later (Boland, personal observations). Extremely high initial densities of seedlings – in part due to the concentrating effect of pleustochory – greatly lessen the importance of high mortality rates.

The effect of pleustochory on seedling densities was obvious at the Goat Canyon pool because the pool was large and unvegetated with a single, isolated seed source. Pleustochory most likely occurs on many water bodies – pools, lakes, even flowing water – when there are source plants nearby, though its effect on seedling densities may be less clear elsewhere. What should be clear at other sites is the effect of pool size. This study showed that the size of the fetch greatly influenced the density of seedlings around the

pool. The size of the fetch was important because all of the seeds that landed on the water within the fetch quickly sailed downwind to the safe site at the water's edge, and a long fetch "collected" more seeds from the seed rain than a short fetch. Consequently there was a positive correlation between fetch size and seedling densities. As size of fetch and size of pool are also positively correlated, it follows that pool size will influence the density of seedlings at a site.

### Pleustochory and Rapid Establishment

It is important for willow seeds to disperse and establish quickly. Willow seeds are small and have no food reserves, so will perish within a few days unless they land in a suitable habitat (Karrenberg et al. 2002). In addition, most willow safe sites on the edges of drying pools are available only temporarily. Therefore, willow seeds need to quickly disperse to safe sites, and pleustochory plays a vital role in their speedy delivery. At the Goat Canyon pool, a *S. gooddingii* seed could be blown from the source stand near the pool in the morning and take approximately five minutes to arrive at the center of the pool 420 m away (i.e., primary dispersal via anemochory). The seed would then take approximately 10 min to sail the 47 m on the pool's surface to the pool's edge (i.e., secondary dispersal via pleustochory). The seed would likely be stalled as long as five hours at the water's edge until the highest waves and wind surges deposit it on the shore, thereby separating the seed from its cottony hairs and placing it in its moist recruitment site where it would start to germinate immediately. Evaporation and the resulting declining water levels would then strand the germinated seed in the moist mud above the new waterline. Fifty percent of the seeds would have germinated within approximately 11 hours of being immersed in the moist mud (Boland unpublished data). In this case, the steps from dispersal of the seed from the parent plant to germination in the recruitment site took less than 24 hours to complete, and this may be typical for willows. Chambers and MacMahon (1994) titled their review of secondary dispersal "A day in the life of a seed" and, although their title implies that they were dealing with processes that occur in a day, they were actually dealing with primary dispersal, secondary dispersal, dormancy and germination in many species where these processes can take months or years. But in *S. gooddingii* all of these processes can really take a single day – probably the most important day in the life of a *S. gooddingii* seed.

### CONCLUSIONS

This paper defines a previously undescribed mode of seed dispersal as pleustochory (dispersal

of seeds by wind while the seeds are floating on water), and distinguishes this mode from anemochory (dispersal of seeds by wind while the seeds are in the air) and from hydrochory (dispersal of seeds downstream by flowing water). The purpose of distinguishing pleustochory from the other two modes of dispersal was to highlight its vital role in three aspects of dispersal: (1) its role in the directed dispersal of willow seeds to their safe sites – the vast majority of *S. gooddingii* seedlings at the Goat Canyon pool were estimated to have arrived via pleustochory; (2) its role in the concentration of seeds (and seedlings) within safe sites – *S. gooddingii* seedlings at the Goat Canyon pool were significantly more dense along the On Shore (where pleustochory had an effect) than along the Off Shore (where it had little or no effect); and (3) its role in the speedy delivery of short-lived seeds into short-lived germination safe sites, allowing *S. gooddingii* seeds to become established in recruitment sites in less than 24 hours after release from the parent plant.

The findings of this paper should also lead us to view pools in a new way, i.e., as collectors and distributors of floating seeds. *S. gooddingii* safe sites are typically rare (comprising less than 0.03% of the flood plain surface area in the Tijuana River Valley during May 2014, Boland unpublished data). Being rare, safe sites are small targets for airborne *S. gooddingii* seeds. But, as this study shows, a pool acts as a collector dish or landing field for seeds that can then sail to safe sites. Because overall pool surface areas are relatively large in relation to those of safe sites (approximately 30 times larger in the flood plain of the Tijuana River Valley in May 2014, Boland unpublished data), pools greatly expand the safe site target area for *S. gooddingii* seeds, thereby increasing the likelihood that seeds will arrive in a site suitable for establishment. Secondary dispersal via pleustochory therefore helps make willows quintessential pioneer plants, as it enables them to quickly arrive and establish in disturbed habitats where conditions for successful germination are rare in both space and time.

#### ACKNOWLEDGMENTS

I thank: Michelle Cordrey at the Tijuana River National Estuary Research Reserve for the wind data, GPS measurements, and producing the maps; Chris Peregrin at California State Parks for making the Goat Canyon area available for study; Lisa Ordóñez for assistance in the field; Deborah Woodward for assistance in the field, helpful discussions, and comments on early drafts of this manuscript; and two anonymous reviewers for thoughtful reviews that greatly improved the manuscript.

#### LITERATURE CITED

- AGUIAR, M. R. AND O. E. SALA. 1997. Seed distribution constrains the dynamics of the Patagonian steppe. *Ecology* 78:93–100.
- AUGSPURGER, C. K. AND S. E. FRANSON. 1988. Input of wind-dispersed seeds into light-gaps and forest sites in a Neotropical forest. *Journal of Tropical Ecology* 4:239–252.
- BOLAND, J. M. 2014. Factors determining the establishment of plant zonation in a southern Californian riparian woodland. *Madroño* 61:48–63.
- BOND, W. J. 1988. Proteas as “tumbleseeds”: wind dispersal through the air and over soil. *South African Journal of Botany* 54:455–460.
- CAMPBELL, D. R., L. ROCHEFORT, AND C. LAVOIE. 2003. Determining the immigration potential of plants colonizing disturbed environments: the case of milled peatlands in Quebec. *Journal of Applied Ecology* 40:78–91.
- CHAMBERS, J. C. AND J. A. MACMAHON. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics* 25:263–292.
- , ———, AND J. H. HAEFNER. 1991. Seed entrapment in alpine ecosystems: effects of soil particle size and diaspore morphology. *Ecology* 72:1668–1677.
- EMERY, D. E. 1988. Seed propagation of native California plants. Santa Barbara Botanic Garden, Santa Barbara, CA.
- FABER, P. A., E. KELLER, A. SANDS, AND B. M. MASSEY. 1989. The ecology of riparian habitats of the southern California coastal region: a community profile. U.S. Department of the Interior, Fish and Wildlife Service, Research and Development National Wetlands Research Center, Biological Report 85 (7.27), Washington, D.C.
- FULLER, R. N. AND R. DEL MORAL. 2003. The role of refugia and dispersal in primary succession on Mount St Helens, Washington. *Journal of Vegetation Science* 14:637–644.
- GAGE, E. A. AND D. J. COOPER. 2005. Patterns of willow seed dispersal, seed entrapment, and seedling establishment in a heavily browsed montane riparian ecosystem. *Canadian Journal of Botany* 83:678–687.
- GLASER, P. H. 1981. Transport and deposition of leaves and seeds on tundra: a late-glacial analogue. *Arctic and Alpine Research* 13:173–182.
- GREENE, D. F. AND E. A. JOHNSON. 1997. Secondary dispersal of tree seeds on snow. *Journal of Ecology* 85:329–340.
- HARPER, J. L. 1977. Population biology of plants. Academic Press, New York, NY.
- HERRERA, C. M. AND P. JORDANO. 1981. *Prunus mahaleb* and birds: the high efficiency seed dispersal system of a temperate fruiting tree. *Ecological Monographs* 51:203–221.
- HOWE, H. F. AND J. SMALLWOOD. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13:201–228.
- JOHNSON, E. A. AND G. I. FRYER. 1992. Physical characterization of seed microsites – movement on the ground. *Journal of Ecology* 80:823–836.
- KARRENBERG, S., P. J. EDWARDS, AND J. KOLLMANN. 2002. The life history of Salicaceae living in the active zone of floodplains. *Freshwater Biology* 47:733–748.
- MAHONEY, J. M. AND S. B. ROOD. 1998. Streamflow requirements for cottonwood seedling recruitment – an integrative model. *Wetlands* 18:634–645.

- MATLACK, G. R. 1989. Secondary dispersal of seed across snow in *Betula lenta*, a gap-colonizing tree species. *Journal of Ecology* 77:853–869.
- NATHAN, R. AND H. C. MULLER-LANDAU. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15:278–285.
- SARNEEL, J. M., B. BELTMAN, A. BUIZE, R. GROEN, AND M. B. SOONS. 2014. The role of wind in the dispersal of floating seeds in slow flowing or stagnant water bodies. *Journal of Vegetation Science* 25:262–274.
- SEIWA, K., M. TOZAWA, N. UENO, M. KIMURA, M. YAMAZAKI, AND K. MATUYAMA. 2008. Roles of cottony hairs in directed seed dispersal in riparian willows. *Plant Ecology* 198:27–35.
- SOKAL, R. R. AND F. J. ROHLF. 1995. *Biometry*. W.H. Freeman and Company, New York, NY.
- SOOMERS, H., D. N. WINKEL, Y. DU, AND M. J. WASSEN. 2010. The dispersal and deposition of hydrochorous plant seeds in drainage ditches. *Freshwater Biology* 55:2032–2046.
- STELLA, J. C., J. J. BATTLES, B. K. ORR, AND J. R. MCBRIDE. 2006. Synchrony of seed dispersal, hydrology and local climate in a semi-arid river reach in California. *Ecosystems* 9:1200–1214.
- STEYN, E. M. A., G. F. SMITH, AND A. E. VAN WYK. 2004. Functional and taxonomic significance of seed structure in *Salix mucronata* (Salicaceae). *Bothalia* 34:53–59.
- TAKEDA, H. 1936. On the coma or hairy tuft on the seed of willows. *The Botanical Magazine, Tokyo* 50:283–289.
- VAN DER PIJL, L. 1982. *Principles of dispersal in higher plants*. Springer-Verlag, New York, NY.
- VAN TOOREN, B. F. 1988. The fate of seeds after dispersal in chalk grassland: the role of the bryophyte layer. *Oikos* 53:41–48.
- VANDER WALL, S. B. AND W. S. LONGLAND. 2004. Diplochory: are two seed dispersers better than one? *Trends in Ecology and Evolution* 19:155–161.
- WATKINSON, A. R. 1978. The demography of a sand dune annual: *Vulpia fasciculata*. III. The dispersal of seeds. *Journal of Ecology* 66:483–498.
- WENNY, D. G. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology Research* 3:51–74.
- AND D. J. LEVEY. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences of the United States of America* 95:6204–6207.
- WETZEL, R. G. 1983. *Limnology*. Saunders, Philadelphia, PA.
- WILLSON, M. F. 1983. *Plant reproductive ecology*. John Wiley and Sons, New York, NY.
- ZEDLER, J. B., C. S. NORDBY, AND B. E. KUS. 1992. *The ecology of Tijuana Estuary, California: a National Estuarine Research Reserve*. NOAA Office of Coastal Resource Management, Sanctuaries and Reserves Division, Washington, D.C.